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A Monte Carlo demographic analysis of the silky shark (*Carcharhinus falciformis*): implications of gear selectivity

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Demographic analysis has recently been used as a tool to approximate the dynamics of shark populations (Caillet, 1992; Sminkey and Musick, 1996; Au and Smith, 1997; Cortés, 1999). The widespread use of demographic models for shark species, however, is hampered by a paucity of information on vital rates, which are required as input parameters for the models. A vital rate of special importance is natural mortality, which remains unknown for most shark species and many other marine taxa. Demographic models thus must often rely on indirect methods of natural mortality estimation rather than empirically observed values specific to a given population. Several methods to estimate natural mortality have shown promise for shark demographic analysis (Cortés, 1998). Other vital rates such as fecundity, although often strongly influenced by size and age, likely also vary independently of time over the lifespan of individuals within a population. Incorporation of Monte Carlo simulation in demographic models has been used to account for some of this uncertainty in vital rate estimates and construct confidence intervals for model output (Cortés, 1999; 2002).

One of the most valuable aspects of demographic modeling is the ability to examine how populations might respond to various levels of fishing

mortality (Au and Smith, 1997; Cortés, 1998; Smith et al., 1998; Simpfendorfer, 1999). To date, most authors have used empirical estimates of fishing mortality (F) and either applied them uniformly to all age groups or have produced various scenarios with F applied starting at a particular age to simulate various fisheries management schemes (Sminkey and Musick, 1996; Au and Smith, 1997; Liu and Chen, 1999). Gear selectivity and its effect on F at various ages, however, has not been incorporated into demographic models even though it is very likely that some selection occurs. Here, we produce a demographic analysis of the silky shark (*Carcharhinus falciformis*) off the southeastern United States. Monte Carlo methods are used to simulate variability in model input parameters, and multiple scenarios are considered, incorporating natural mortality only, and added fishing mortality components. We include in our analysis scenarios that reflect possible longline gear selectivity for silky sharks, using catch-at-age information estimated from length-frequency data provided by the U.S. pelagic longline observer program for the southeastern U.S. coast. Finally, we compare scenarios that incorporate the same mean value of fishing mortality, but with different assumptions of selectivity patterns. The results of the demographic

analysis are discussed in the context of the robustness of model assumptions.

Materials and methods

Life history parameters for the silky shark demography were obtained from the best available literature sources. Von Bertalanffy parameters of $L_{\infty} = 311$ cm total length, $K = 0.101/\text{yr}$, and $t_0 = -2.718$ yr were taken from Bonfil et al. (1993). To account for some of the uncertainty in the estimate of age-at-maturity (t_{mat}) of 12 years given by Bonfil et al. (1993), values for t_{mat} were drawn at random from a discrete probability distribution of $P = 0.25$, 0.5 , and 0.25 for ages 11, 12, and 13, respectively. Longevity (t_{max}) was similarly varied by assigning the estimate of Bonfil et al. (1993) of 22 years a $P = 0.5$ and linearly decreasing P by 50% for each subsequent year.

Estimates of natural mortality (M) were selected by using three methods: Peterson and Wroblewski (1984), Chen and Watanabe (1989), and Jensen (1996) (Table 1). For the Peterson and Wroblewski method, weights-at-age were determined by calculating total length-at-age from the von Bertalanffy growth function, and then converting these values to fork length and weight (in grams) by using the relationships given by Kohler et al. (1995) for the silky shark. Wet weight was used instead of dry weight to generate values of M . Annual survival (S_x ; $S_x = e^{-M}$, $x = \text{age}$) values were randomly drawn from a distribution in which the three methods of calculating mortality rates had equal probability.

Fecundity (m_x), the number of female pups produced per each year of life, was calculated by combining the data of Fourmanoir (1961), Bane (1966), Gilbert and Schlernitzauer (1966), Branstetter (1987), and Bonfil et al. (1993), which yielded a mean of 10.3 (SD=2.213, $n=16$) pups per litter. Observations in the literature of litter sizes lower than five pups were not included because of the possibility that females might have aborted pups from one uterus during capture

Table 1

Natural mortality (M) estimation methods used in demographic models for silky sharks (*Carcharhinus falciformis*). W = body weight in grams, K , t_0 = von Bertalanffy growth parameters, and t_{\max} = maximum age.

Citation	Method
Peterson and Wroblewski (1984)	$M = 1.92 W^{-0.25}$
Jensen (1996)	$M = 1.6K$
Chen and Watanabe (1989)	$M(t) = K/[1 - e^{-K(t-t_0)}]$, for $t = 0$ through 11 $M(t, t_{\max}) = [1/(t_{\max} - t)] \ln [(e^{Kt_{\max}} - e^{Kt_0})/(e^{Kt} - e^{Kt_0})]$

(Branstetter, 1987; Bonfil et al., 1993). Pups-per-litter estimates were then converted into female pups per year (m_x) by using the embryo sex ratio of 1:1.17 (male:female) given by Bonfil et al. (1993) and a reproductive cycle of two years suggested by Branstetter (1987). All females were assumed to enter the breeding population after first age-at-maturity, and reproductive senescence was assumed to occur at age ($t_{\max}+1$). Actual values of fecundity (m_x) used as model input were drawn at random from a normal distribution with a mean of 10.3 and a standard deviation of 2.213 calculated as described above, and then scaled to represent female pups per year.

The parameters estimated above were used to construct life tables by using standard methods, but incorporating Monte Carlo simulation for output parameter estimation. Output parameters (net reproductive rate, R_0 ; mean generation length, G ; and intrinsic rate of population increase, r) were calculated by standard demographic methods (Wilson and Bossert, 1971; Krebs, 1985), and r was solved iteratively with the Euler equation.

Various scenarios, each of which varied vital rates as described above, were analyzed. A base scenario incorporated natural mortality only. To attempt to incorporate gear selectivity, we compared a model that incorporated total mortality only (Z , scenario 1) estimated from a traditional catch curve with a model incorporating Z estimated from a modified catch curve method. To produce a catch curve estimate of Z , length-frequency data for silky sharks observed on longlines off the southeastern United States during 1992–98 (NMFS¹) were used with an age-length key derived from the length-at-age data of Bonfil et al. (1993). The assumptions in this method are that in all years 1) recruitment is constant, 2) fishing mortality is constant, and 3) catchability is equal (there is no gear selectivity). The decrease in population over time is

$$N_t = N_{t-1} e^{-Za},$$

where N_t = population in numbers at time t ; and
 a = age.

An assumption of gear selectivity was then used to modify the standard catch equation. If one assumes that gear selectivity exists, then Z can no longer be constant and Z can be estimated at each age:

$$-Z = \ln(N_t / N_{t-1}) / a.$$

To avoid positive values of Z at some ages (due to those ages not being present in the catch as predicted by the age-length key) an exponential curve was fitted to the catch-at-age data to produce the values of N_t . Because the value of Z cannot be calculated for age 0 with this method, we assumed that total mortality was the same for ages 0 and 1. The values of Z -at-age produced by this method were used in a demographic model (scenario 2) and compared with scenario 1. For ages where estimates of Z were not reasonable ($Z < M$), the natural mortality estimate was used for that age.

To examine the effect of various patterns of selectivity, we also compared scenarios with the same average value of fishing mortality, but with various assumptions of selectivity patterns. These scenarios added a fishing mortality component into the base scenario. Scenario 3 incorporated the 1997 instantaneous fishing mortality (F) value of 0.093 estimated for Atlantic large coastal sharks (Anonymous²) applied uniformly to all age groups. An exponential function of the form $y = be^{(-ax)}$, where $y = F$, x = age, and the mean $F = 0.093$, was fitted to the catch-at-age data assuming zero fishing mortality after age 13 (scenario 4) and a positive level of fishing mortality through all age groups (scenario 5). Scenario 6 applied an F value of 0.034, calculated to produce maximum sustainable yield (MSY) for large coastal sharks (Anonymous²), uniformly to all age groups. Scenarios 7 and 8 were constructed in the same manner as scenarios 4 and 5, respectively, but with the mean value of $F = 0.034$.

Each of the scenarios were run 1000 times with vital rates (first age-at-maturity, fecundity, longevity, and natural mortality where appropriate) varying as described above. The 2.5th and 97.5th percentiles of the ranked output were used as approximate percentile confidence

¹ NMFS (National Marine Fisheries Service). 2000. Unpubl. data. Southeast Fisheries Science Center Pelagic Observer Program, 75 Virginia Beach Drive, Miami, FL 33149.

² Anonymous. 1998. Report of the shark evaluation workshop, 109 p. Panama City Laboratory, National Marine Fisheries Service, 3500 Delwood Beach Rd., Panama City, FL 32408.

intervals for the parameters R_0 , G , and r . Finite rates of population increase or decrease (e^r) and approximate percentile confidence intervals were then calculated based on the r value output. All simulations were run by using Microsoft Excel spreadsheet software.

Results

The three methods used to estimate natural mortality yielded annual survivorship (S) values ranging from 0.657 to 0.904 (Table 2). The method of Peterson and Wroblewski produced S values of 0.760 (age 0) to 0.904 (age 22), slightly higher than the values produced by the method of Chen and Watanabe (0.657 to 0.874, ages 0–11; 0.890, ages 12+). The method of Jensen produced the lowest S value (0.851) for ages 7 and above, and the highest survivorship in the first 4 years of life.

The catch-at-age histogram indicated that few silky sharks over the age of 7 years were caught in the southeastern pelagic longline fishery (Fig. 1). The catch curve estimated a Z value of 0.329 ($r^2=0.838$, Fig. 2). The Z -at-age values calculated from the modified catch curve method predicted values of $Z = 0$ for ages 12 and above (scenario 2; Table 3). Values of F -at-age used in scenarios 3–8 (Table 3) were as high as 0.287 (scenario 4, age 0).

The results of the base scenario (Table 4) indicated that the silky shark population, in absence of fishing mortality, would increase at a median rate of 4.9 %/yr. The approximate percentile lower confidence limit also showed positive population growth ($e^r=1.027$). Incorporating the Z obtained from the catch curve into the model (scenario 1) resulted in the greatest rate of population decline of any of the scenarios considered ($e^r=0.895$). However, the use of the Z -at-age values from the modified catch curve method (scenario 2) produced a positive population increase of 1.8 %/yr.

With estimated F for large coastal sharks in 1997 applied to all age groups (scenario 3), the population would decline at a rate of 4.4 %/yr. Application of exponentially decreasing fishing mortality resulted in a more optimistic median e^r value when the mean F was confined to ages 0–12 (scenario 4), but when mean F was applied to all ages (scenario 5), the output was more pessimistic than that for the constant $F = 0.093$ model. With F estimated for maximum sustainable yield (scenario 6), the silky shark population would slowly increase at a rate of 1.5 %/yr. Incorporation of variable F -at-age in scenarios 7 and 8 resulted in e^r values slightly higher and lower, respectively, than the constant F scenario.

Discussion

The base scenario results given in our study match well those from other demographic models for silky sharks. Using a demographic model that incorporated density-

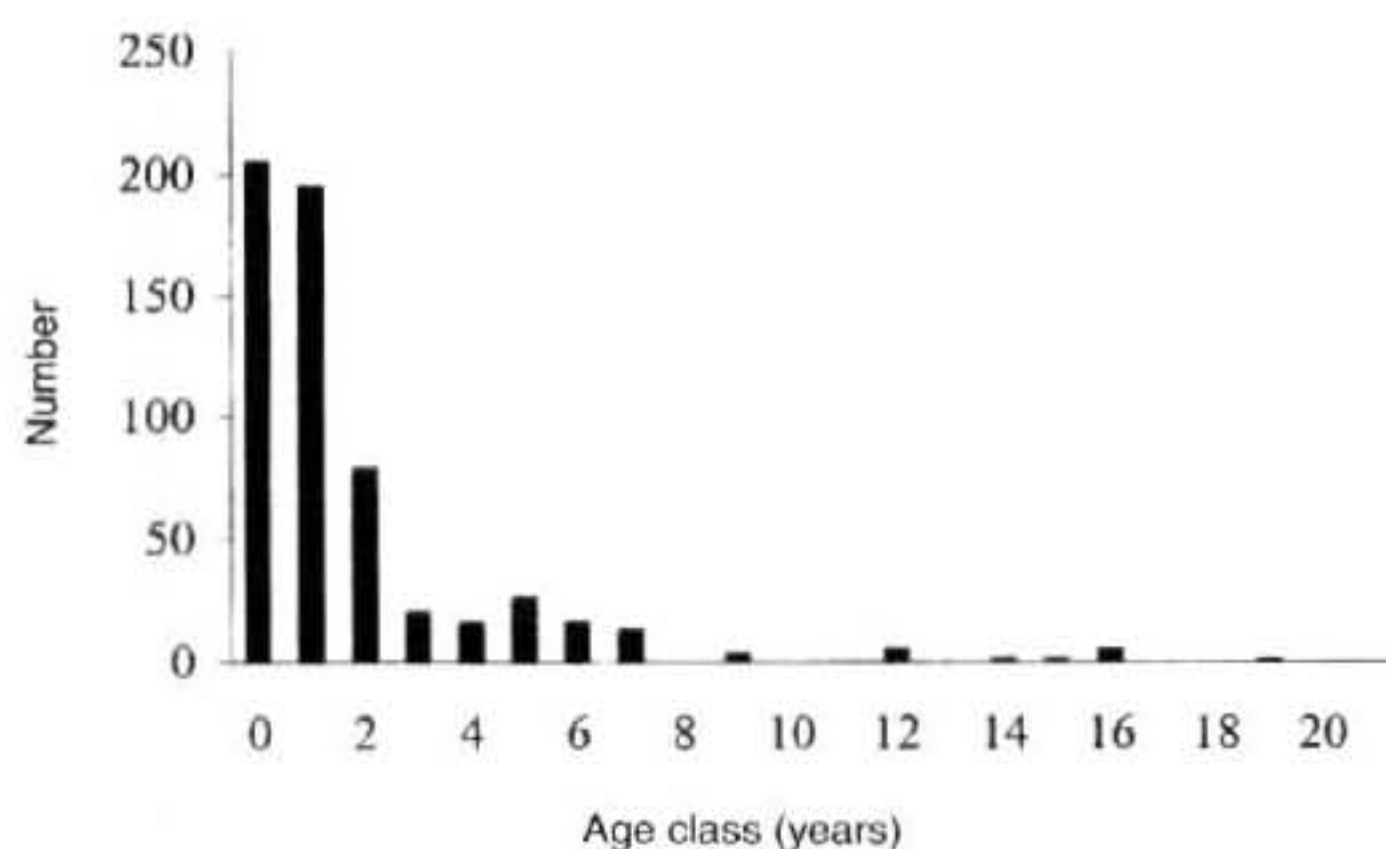


Figure 1

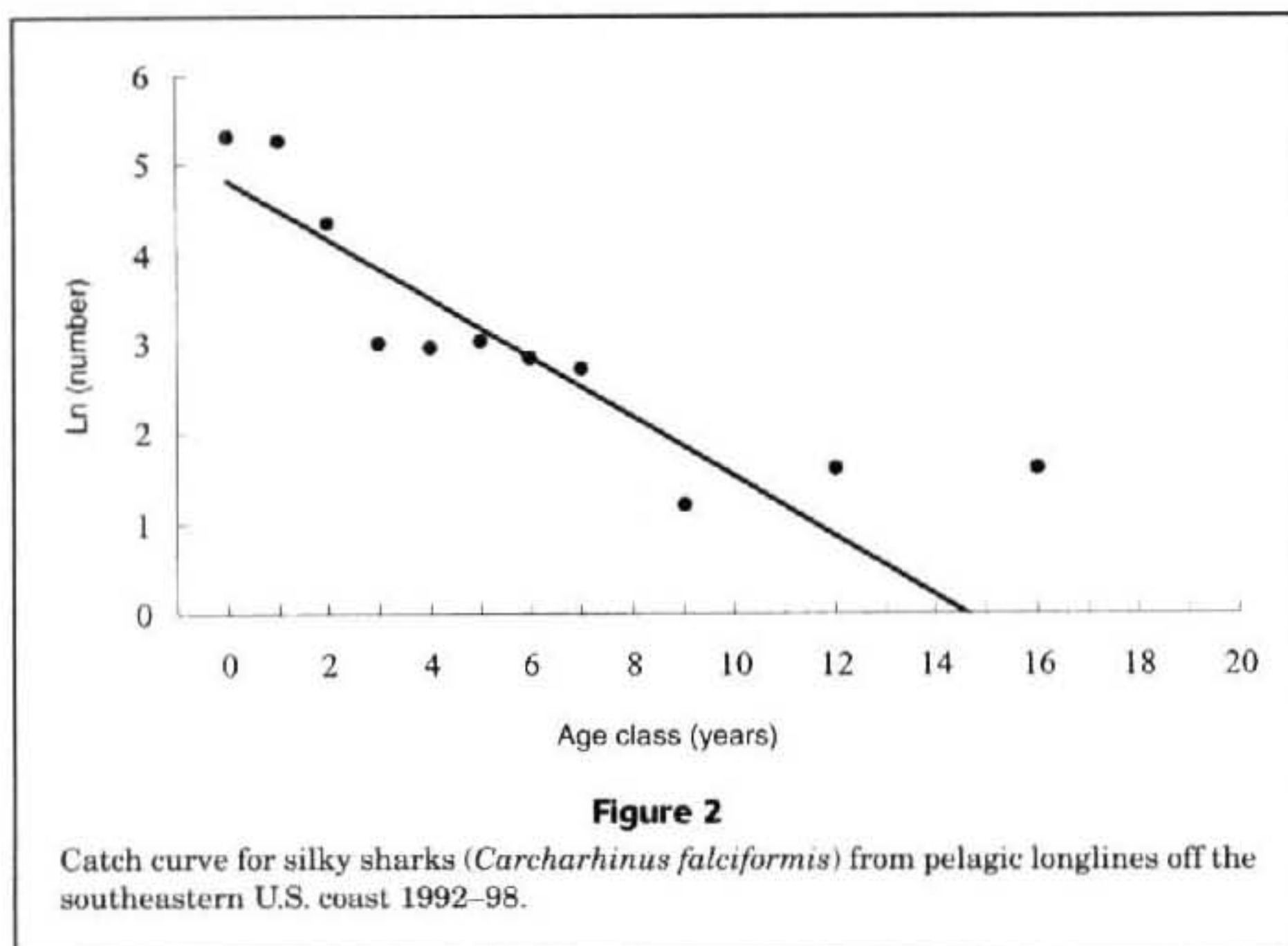
Estimated silky shark (*Carcharhinus falciformis*) catch-at-age from pelagic longlines off the southeastern U.S. coast, 1992–98.

Table 2

Annual survivorship (S) estimates calculated from three studies based on best available life history information for the silky shark (*Carcharhinus falciformis*).

Age (yr)	Peterson and Wroblewski	Chen and Watanabe	Jensen
0	0.760	0.657	0.851
1	0.799	0.724	0.851
2	0.824	0.766	0.851
3	0.840	0.794	0.851
4	0.853	0.815	0.851
5	0.862	0.830	0.851
6	0.869	0.842	0.851
7	0.875	0.851	0.851
8	0.880	0.858	0.851
9	0.884	0.865	0.851
10	0.887	0.870	0.851
11	0.890	0.874	0.851
12	0.892	0.890	0.851
13	0.894	0.890	0.851
14	0.896	0.890	0.851
15	0.898	0.890	0.851
16	0.899	0.890	0.851
17	0.900	0.890	0.851
18	0.901	0.890	0.851
19	0.902	0.890	0.851
20	0.903	0.890	0.851
21	0.904	0.890	0.851
22	0.904	0.890	0.851

dependence, Smith et al. (1998) found an r value of 0.043 for silky sharks. Cortés (2002) found an average r value of 0.055 for silky sharks from the southern Gulf of Mexico



using density-independent matrix simulation models. These r values place the silky shark toward the middle of the range of productivity values calculated for a mix of species (Smith et al., 1998; Cortés, 2002).

The pessimistic results of the model that incorporated Z calculated from the catch curve are consistent with the stock assessments that indicate large coastal sharks are overfished and suggest, in particular, that exploitation rates in the pelagic longline fishery may not be sustainable for silky sharks. However, incorporating gear selectivity with the modified catch curve method altered the results, yielding one of the highest rates of population growth of any of the scenarios. If the assumptions about the relationship between the catch curve and selectivity are reasonable, the results indicate that incorporation of gear selectivity into demographic analysis is important.

The importance of considering selectivity as explored by the fishing mortality scenarios was less clear. Scenario 3 indicated that a recently estimated level of fishing mortality would produce declines in the population, whereas scenario 6 indicated that the fishing mortality level producing maximum sustainable yield would result in a slightly increasing population. When exponentially decreasing F -at-age was incorporated (scenarios 4, 5, 7, and 8), the results differed—but much less so than those of scenarios 1 and 2—from those obtained in the constant F scenarios (3 and 6). All the fishing mortality scenarios (3–8) used mean values of F estimated through density-dependent modeling and were used here only as comparative base values.

Stock assessments of northwestern Atlantic shark stocks are based on species groups rather than individual species. These assessments use data from fisheries of various gear types, which may not correctly represent the life history or the pattern of exploitation of an individual species. In that respect, *Carcharhinus falciformis* may be an

excellent example. Off the coast of the southeastern United States, pelagic longlines may be the dominant cause of silky shark fishing mortality, whereas bottom longlines rarely capture, and drift gillnets do not capture, this species (Parrack et al., 1993; Trent et al., 1997). Examination of length frequencies from the pelagic longline fishery observer database suggests that age 8+ silky sharks are rarely caught. Therefore, the assumption of constant fishing mortality throughout all age groups for this species is probably invalid, at least for the pelagic fishery off the southeastern United States. If individual species management of silky sharks is ever to become a reality, the patterns of selectivity of longline gear are very important.

It seems logical that the larger the shark, the higher the probability it can bite through the monofilament gangions used by U.S. pelagic longliners and escape. Because size is correlated with age, there must be a functional relationship that describes the probability of retention and capture for a given age. Accurate elucidation of such gear selectivity patterns requires knowledge of the actual size-at-age characteristics of the population that can only be derived from sampling studies in which methods that are not size-selective are used, or that are at least less size-selective than longline gear. These types of comparative data are almost wholly lacking for sharks in the pelagic environment. Indirect methods of estimating selectivity for shark species by comparing catches from gillnets of various mesh sizes have shown promise (Kirkwood and Walker, 1986; Simpfendorfer and Unsworth, 1998). Previous indirect studies of selectivity in hook and line gear (Cortez-Zaragoza et al., 1989; Ralston, 1990) cannot be applied in this case because selectivity in those studies was described as a function of hook size rather than the actual breaking strength of the line, which is the speculated mechanism of selection in the present study. Walker

Table 3

Values of total mortality (Z) or fishing mortality (F) used in demographic models for the silky shark (*Carcharhinus falciformis*). For scenario 1, Z was used instead of estimates of natural mortality (M). In scenario 2, Z was used only when $Z > M$. In scenarios 3–8, F was added to natural mortality.

Age (yr)	Scenario							
	1 Z	2 Z	3 F	4 F	5 F	6 F	7 F	8 F
0	0.329	0.486	0.093	0.287	0.276	0.034	0.105	0.068
1	0.329	0.486	0.093	0.210	0.225	0.034	0.077	0.058
2	0.329	0.243	0.093	0.164	0.195	0.034	0.060	0.053
3	0.329	0.162	0.093	0.132	0.174	0.034	0.048	0.049
4	0.329	0.121	0.093	0.107	0.158	0.034	0.039	0.046
5	0.329	0.097	0.093	0.087	0.144	0.034	0.032	0.043
6	0.329	0.081	0.093	0.069	0.133	0.034	0.025	0.041
7	0.329	0.069	0.093	0.054	0.123	0.034	0.020	0.040
8	0.329	0.061	0.093	0.041	0.114	0.034	0.015	0.038
9	0.329	0.054	0.093	0.029	0.107	0.034	0.011	0.037
10	0.329	0.049	0.093	0.019	0.100	0.034	0.007	0.035
11	0.329	0.044	0.093	0.009	0.093	0.034	0.003	0.034
12	0.329	0.000	0.093	0.09×10^{-5}	0.087	0.034	0.09×10^{-5}	0.033
13	0.329	0.000	0.093	0.000	0.082	0.034	0.000	0.032
14	0.329	0.000	0.093	0.000	0.077	0.034	0.000	0.031
15	0.329	0.000	0.093	0.000	0.072	0.034	0.000	0.030
16	0.329	0.000	0.093	0.000	0.068	0.034	0.000	0.029
17	0.329	0.000	0.093	0.000	0.063	0.034	0.000	0.029
18	0.329	0.000	0.093	0.000	0.059	0.034	0.000	0.028
19	0.329	0.000	0.093	0.000	0.056	0.034	0.000	0.027
20	0.329	0.000	0.093	0.000	0.052	0.034	0.000	0.026
21	0.329	0.000	0.093	0.000	0.049	0.034	0.000	0.026
22	0.329	0.000	0.093	0.000	0.045	0.034	0.000	0.025
23	0.329	0.000	0.093	0.000	0.042	0.034	0.000	0.025
24	0.329	0.000	0.093	0.000	0.039	0.034	0.000	0.024
25	0.329	0.000	0.093	0.000	0.036	0.034	0.000	0.024
26	0.329	0.000	0.093	0.000	0.034	0.034	0.000	0.023
27	0.329	0.000	0.093	0.000	0.031	0.034	0.000	0.023
28	0.329	0.000	0.093	0.000	0.028	0.034	0.000	0.022
29	0.329	0.000	0.093	0.000	0.026	0.034	0.000	0.022

(1992) incorporated hook selectivity into an age-structured model, but he assumed that all recruited members of a stock had an equal value of catchability with longline gear. We believe that an assumption of equal catchability is incorrect for silky sharks, and sharks in general, hooked on monofilament pelagic longline gear.

Determining actual patterns of selectivity and resulting estimates of fishing mortality-at-age, however, was beyond the scope of our analysis, which was to suggest that patterns of gear selectivity can affect results from demographic models. We chose a simple modification of a traditional catch curve and an intuitive, although arbitrary, assumption of selectivity patterns for silky sharks on pelagic longlines to explore this effect. Arbitrarily derived

selectivity schedules were employed previously to examine the potential effects of gear selection in yield-per-recruit models (Goodyear, 1996). Clearly this approach, as applied here, has limitations. For example, the curve fitted to catch-at-age data used to calculate Z values estimated zero total mortality at ages 12+, whereas the catch-at-age data showed a few captures of ages 12+ (Fig. 1). No mortality is assumed for individual animals that escape the gear, although it is possible that some animals may die. Despite shortcomings in the methods to estimate F -at-age values used in our study, better estimates of fishing mortality will require more robust, comparative selectivity data.

Like many other studies of shark populations, the results reported in our study must be considered preliminary

Table 4

Demographic output (R_0 =net reproductive rate; G =mean generation length; r =intrinsic rate of population growth; e^r =finite rate of population growth) and lower (LCL) and upper (UCL) approximate confidence limits for the silky shark (*Carcharhinus falciformis*) off the southeastern U.S. coast. The base scenario incorporated natural mortality (M) only; scenario 1 incorporated a constant value of total mortality (Z), scenario 2 incorporated various values of Z -at-age, and scenarios 3–8 incorporated the mean value of fishing mortality (F) shown in the second column.

Scenario	Mean F (or Z)	R_0	LCL	UCL	G	LCL	UCL	r	LCL	UCL	e^r	LCL	UCL
base	none	2.161	1.547	2.959	16.115	14.942	17.570	0.048	0.027	0.071	1.049	1.027	1.074
1	0.329	0.195	0.127	0.284	14.380	13.266	15.484	-0.111	-0.130	-0.091	0.895	0.878	0.913
2	0.065	2.615	2.083	3.158	16.091	14.965	17.582	0.018	0.001	0.032	1.018	1.001	1.033
3	0.093	0.508	0.345	0.724	15.190	14.042	16.544	-0.044	-0.066	-0.022	0.957	0.936	0.978
4	0.093	0.652	0.477	0.886	16.113	14.946	17.546	-0.026	-0.045	-0.008	0.974	0.956	0.992
5	0.093	0.262	0.175	0.375	15.427	14.235	16.857	-0.084	-0.105	-0.066	0.919	0.900	0.936
6	0.034	1.266	0.898	1.747	15.755	14.605	17.176	0.015	-0.006	0.037	1.015	0.994	1.038
7	0.034	1.392	0.991	1.920	16.105	14.937	17.565	0.021	-0.001	0.043	1.021	0.999	1.044
8	0.034	1.130	0.783	1.539	15.815	14.623	17.261	0.008	-0.015	0.029	1.008	0.985	1.029

because of the lack of validated age and growth information and the uncertainty in the estimates of longevity and fecundity for the silky shark. It is difficult to determine how representative the von Bertalanffy parameters (Bonfil et al., 1993), which were derived from silky sharks in the Campeche Bank in the southern Gulf of Mexico, are for silky shark populations from the entire southeastern U.S. Atlantic. Although tagging data (Kohler et al., 1998) indicate movement of silky sharks between the Gulf of Mexico and the U.S. Atlantic coast, the small number of tagged and recaptured individuals makes firm conclusions about whether these are the same or separate stocks very difficult. The age and growth results of Bonfil et al. (1993) from the southern Gulf of Mexico differed from a study on silky sharks by Branstetter (1987) in the northern Gulf. It is possible, however, that these variations may be a result of methodological or sampling differences because Branstetter's (1987) data came from pelagic longline operations and had fewer specimens over 250 cm TL, compared to Bonfil et al.'s (1993) data which came mainly from specimens caught in gillnet fisheries. Even if migration of silky sharks occurs between the northern Gulf of Mexico, southern Gulf of Mexico, and southeastern U.S. Atlantic coastal region, the populations of sharks in these areas might have significant life history differences. Given the absence of age and growth studies from Atlantic silky sharks, the Gulf of Mexico studies must be regarded as the best available age and growth information for this species. Similarly, fecundity and longevity estimates are relatively uncertain. Especially important in fecundity estimates is information regarding age-specific birth rate and the possibility of reproductive senescence, which can affect demographic results.

As with other demographic analyses, theoretical estimates of natural mortality (M) were used in our study. It has been shown that the output of demographic models of shark populations is particularly sensitive to changes in M , especially during the first few years of life (Sminkey

and Musick, 1996; Liu and Chen, 1999; Cortés, 2002). Moreover, results may vary considerably in analyses that use different methods of M estimation (Simpfendorfer, 1999). In recognition of these limitations, three different methods were used here to estimate M . The methods of Chen and Watanabe (1989) and Jensen (1996) are based on a relationship between M and growth rates. Because the age and growth information for silky sharks is unvalidated, the von Bertalanffy growth parameters used in our study may not adequately describe individuals from the population analyzed. Finally, the method of Peterson and Wroblewski (1984) involves the assumption that M is due primarily to predation. Although this may be true for the younger ages of large coastal sharks like the silky shark, it may not be true for the larger, older sharks. Additionally, wet weight was used instead of dry weight, as prescribed in the original equation of Peterson and Wroblewski (1984), because the estimates of M obtained by using wet weight seem more believable for sharks (Cortés, 2002). Despite the difficulties associated with all three methods of estimating natural mortality, these methods, together with catch curves and tag-recapture studies, are the only methods available for estimating M . The use of Monte Carlo simulation to randomly vary the estimates of natural mortality can account for some of the uncertainty associated with these methods (Cortés, 1999; 2002).

Conclusions from this analysis of the silky shark population off the southeastern U.S. coast are similar to those for other large shark species. Even under scenarios assuming natural mortality only, the population would grow at a fairly slow rate, and even moderate levels of fishing mortality might produce population declines. Inclusion of age-dependent patterns of fishing mortality into the analyses, however, appear to substantially affect model results. Several key elements that need to be clarified to obtain a more conclusive analysis for silky sharks include validated age and growth information, life history param-

eters such as longevity, fecundity, and natural mortality, and estimates of age-dependent fishing mortality.

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